

New information on *Dianmeisaurus gracilis* Shang & Li, 2015

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Abstract *Dianmeisaurus gracilis* is restudied on the basis of a new specimen. It provides some new information, especially that on the skull roof, to the species. The most striking of those new characters include the snout (preorbital region) shorter than the orbit, the interorbital septum extremely narrow, the frontal with a sharp process at both ends, and the posterior margin of the skull roof deeply V-shaped. A phylogenetic analysis with new information confirms that *Dianmeisaurus* is the sister group of *Diandongosaurus* and that these two genera, together with those Chinese taxa (*Majiasanosaurus*, *Dianopachysaurus*, *Keichousaurus*, and *Dawazisaurus*), form a monophyletic clade which is more closely related to the Nothosauroidae than to a clade formed by the European pachypleurosaurs.

Key words Luoping, Yunnan, China; Anisian, Middle Triassic; small sized eosauroptrygian, *Dianmeisaurus gracilis*

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1 Introduction

Dianmeisaurus gracilis is a small-sized eosauroptrygian (Shang and Li, 2015). The holotype of the taxon was collected from Member II (Anisian) of the Guanling Formation in Luoping County of Yunnan Province, China. The previous work suggested that *Dianmeisaurus* was closely related to *Diandongosaurus* from the same stratum of Luoping (Shang and Li, 2015). Together with *Dianopachysaurus dingi* (Liu et al., 2011), *Diandongosaurus acutidentatus* (Shang et al., 2011), and *Dawazisaurus brevis* (Cheng et al., 2016), four small-sized eosauroptrygians have been reported so far from Member II of the Guanling Formation in Luoping.

Unfortunately, the holotype of *Dianmeisaurus* lacks information on the dorsal side of the skeleton owing to only the ventral side of the skeleton visible. Here we report a new specimen of *Dianmeisaurus gracilis* from its type locality, which is nearly complete and preserved in dorsal view. Thus additional osteological features from the dorsal side of the skeleton can be observed. With new information, the new specimen enriches our knowledge

of *Dianmeisaurus*, helps to clarify its phylogeny based on the holotype, and tests the existing hypotheses on phylogenetic relationships among the European pachypleurosaurs (including the *Neusticosaurus*, *Serpianosaurus*, *Dactylosaurus* and *Anarosaurus*), Nothosauroida, and the Chinese pachypleurosaur-like forms (sensu Cheng et al., 2016).

2 Description

The new specimen (IVPP V 17054) is fully articulated and preserved in dorsal view (Fig. 1). It is nearly complete, with a length of 250 mm, and slightly smaller than the holotype, which has total length of 315 mm.

The following description on the dorsal side of the species is based on the new specimen. We also give some description on the ventral side of the species based on the holotype to compare.

Skull The length of the skull (from the tip of the snout to the occipital condyle) is 18.5 mm in the new specimen (Fig. 2), slightly shorter than that of the holotype (22 mm). The snout (preorbital region) is very short and even shorter than the orbit in length, which is comparable to the condition of *Keichousaurus hui* among known eosauroptrygians (Holmes et al., 2008). It is round anteriorly and lacks rostral constriction.

The oval-shaped external naris is very small and sitting anteriorly, closer to the snout end than to the orbit, which is in contrast to that seen in *Dianopachysaurus dingi* (Liu et al., 2011) and *Dawazisaurus brevis* (Cheng et al., 2016) where the opposite is true.

The orbit is large, slightly longer than wide. Its longitudinal length is slightly less than twice length of the supratemporal fenestra. The supratemporal fenestra is elongated elliptic in outline as in *Dianopachysaurus* and *Dawazisaurus* but differs from the oval-shaped of *Diandongosaurus* (Shang et al., 2011). The infratemporal fenestra is large and opens ventrally as in the aforementioned taxa. The oval pineal foramen is positioned anteriorly, setting at a level about the anterior margin of the supratemporal fenestra.

As in *Dianopachysaurus* and *Dawazisaurus*, the preorbital region is shorter than the postorbital portion (to the posterolateral end of the squamosal). *Dianmeisaurus* differs from

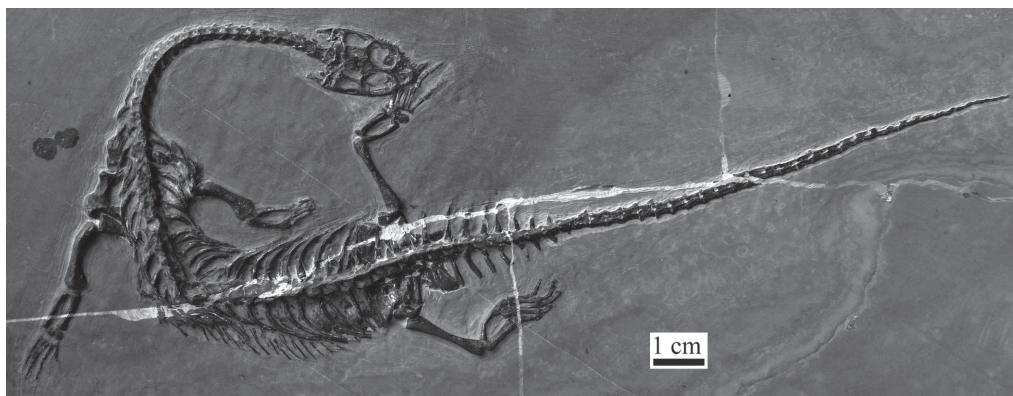


Fig. 1 Skeleton of *Dianmeisaurus gracilis* (IVPP V 17054) in dorsal view

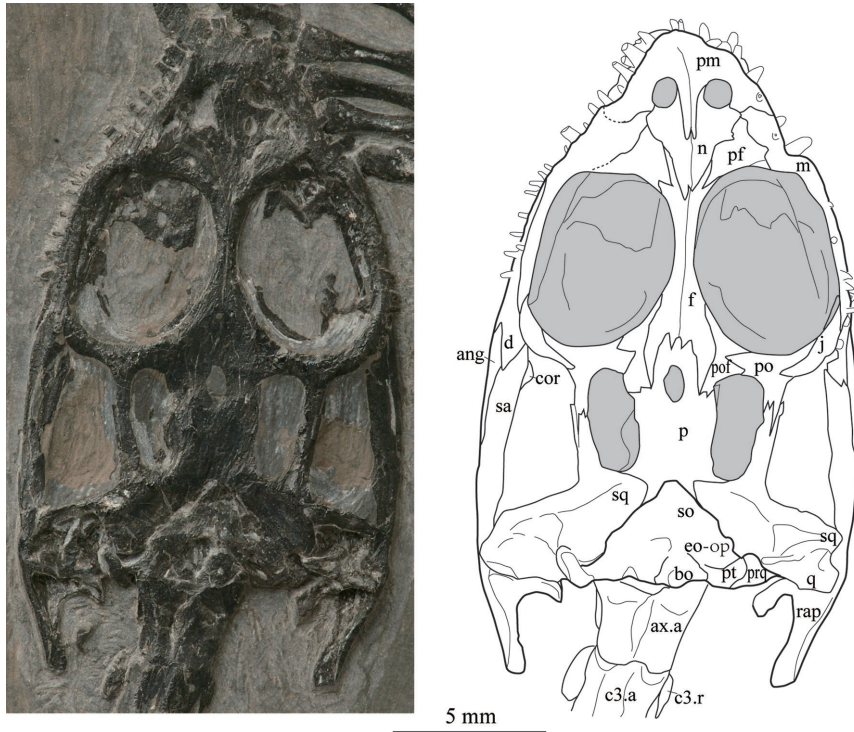


Fig. 2 Photo and outline of the skull and mandible of *Dianmeisaurus gracilis* (IVPP V 17054) in dorsal view

Abbreviations: ang. angular 隅骨; ax.a. axial neural arch 枢椎椎弓; bo. basioccipital 基枕骨; c3.a. the 3rd cervical vertebral neural arch 第3节颈椎椎弓; c3.r. the 3rd cervical rib 第3颈肋; cor. coronoid 冠状骨; d. dentary 齿骨; eo-op. exoccipital-opisthotic 外枕骨-后耳骨; f. frontal 额骨; j. jugal 轭骨; m. maxilla 上颌骨; n. nasal 鼻骨; p. parietal 顶骨; pf. prefrontal 前额骨; pm. premaxilla 前颌骨; po. postorbital 眶后骨; pof. postfrontal 后额骨; prq. pterygoid ramus of quadrate 方骨翼骨支; pt. pterygoid 翼骨; q. quadrate 方骨; rap. retroarticular process 反关节突; sa. surangular 上隅骨; so. supraoccipital 上枕骨; sq. squamosal 鳞骨

them in that the interorbital septum is extremely narrow, less than 1/3 of the interfenestral region of skull table in width. The occipital edge of the skull roof is deeply concave as in *Dawazisaurus*.

The large, paired premaxillae form most of the snout. It embraces the external naris and shapes the anterior and lateral margin of the external naris. Its maxillary process extends posteriorly and contacts the maxilla posteriorly and the nasal posteromedially at the level behind the posterior margin of the external naris. Its nasal process is elongate and extends further posteriorly between the nasals to a level far behind the posterior margin of the external naris. The palatal portion of the premaxilla is largely covered by the mandible in the holotype, but it is clear that the bone meets its counterpart along the ventral midline and forms the entire anterior margin of the internal choana. Posteriorly, the premaxilla contacts the maxilla laterally and the vomer medially. This situation is same as the European pachypleurosaurs and *Keichousaurus* (Sander, 1989; Carroll and Gaskill, 1985; Holmes et al., 2008), but differs from the *Diandongosaurus* (Sato et al., 2014) and *Nothosaurus* (Rieppel, 2000: figs. 55B, 58B, 59B,

60B) in which the premaxilla is excluded from the internal naris.

The nasals meet each other posteriorly along the midline. Anteriorly, they have a slender premaxillary process, which extends anteriorly into the external naris and further lines the medial margin of the naris against the nasal process of the premaxilla. In other words, the premaxillary process of the nasal and the nasal process of the premaxilla together form the internarial septum. Posteriorly, the nasals taper off and end between the anterior processes of the frontals at a level shortly behind the anterior margin of the orbit. Laterally, the nasal forms the posterior margin of the external naris and meets the maxillary process of the premaxilla, which excludes the maxilla from the naris.

The dorsal exposure of the prefrontal is broad. Its anterior process inserts between the nasal and maxilla, approaching the sutural joint of the premaxilla, nasal and maxilla. Sutures with the nasal and maxilla are zig-zagged and the prefrontal-frontal suture is deeply interdigitated.

The paired frontals form the dorsal margins of the orbits. The interorbital septum is extremely narrow in the new specimen as shown in the holotype where a wide split along the ventral midline exposed the ventral surface of the frontals (see Shang and Li, 2015: fig. 2). The anterior end of the frontal tapers into a sharp process, which embraces, together with its counterpart from the other side, the nasals anteriorly, and laterally, the sharp process is forked to receive the prefrontal. Posteriorly, the frontal also tapers into a sharp process to embrace, together with its counterpart of the other side, the parietal and approaches the supratemporal fossa posteriorly as in many other Chinese pachypleurosaur-like forms such as *Dianopachysaurus* (Liu et al., 2011), *Diandongosaurus* (Shang et al., 2011), and *Dawazisaurus* (Cheng et al., 2016). The frontal-postfrontal suture is slightly convex laterally, while the frontal-parietal suture is deeply interdigitated.

As in *Dianopachysaurus*, *Dawazisaurus* and *Diandongosaurus*, the postfrontal broadly lines the posteromedial margin of the orbit anterolaterally and enters anteromedial margin of the supratemporal fenestra posterolaterally. Sutures with the parietal and postorbital are interdigitated.

The maxilla does not take part in the formation of the ventral margin of external naris. It meets the premaxilla at a level behind the posterior margin of the external naris. The ascending process of the maxilla is not well-developed. Posteriorly, the maxilla forms the entire ventral margin of the orbit and overlapped by the jugal at the level of the posteroventral corner of the orbit.

The jugal is a small, lunate-like bone. It forms the posteroventral margin of the orbit, ending anteriorly at a level just posterior to the midpoint of the ventral orbital margin. Posteriorly, the jugal forms the anterior margin of the infratemporal fenestra but is excluded from the upper temporal arch.

The postorbital is a triradiate element. Anteriorly, it defines the posterior border of the orbit. Its anteromedial ramus forms most of the orbital-supratemporal septum. Its posterior ramus extends caudally to a level slightly anterior to the midpoint of the supratemporal arch.

Its suture with the jugal is lineal while its suture with the squamosal is deeply interdigitated.

The parietals are fully fused in new specimen, but their anterior portions anterior to the parietal foreman are sutured in ventral view in the larger holotype, which may indicate a variation in *Dianmeisaurus*. The parietal is extremely broad and flat between the supratemporal fenestrae and lacks a constriction at the posterior-most portion, which is seen in *Dianopachysaurus*, *Dawazisaurus* and *Keichousaurus*. Starting from the parietal foreman, the parietal narrows as a process inserting between the posterolateral processes of the frontals. The parietal broadens posterolaterally and meets the squamosal in an oblique but lineal suture, and posteriorly, its occipital margin is very concave as in *Dawazisaurus*.

The squamosal is a large and stout element. Anteriorly, it forms the posterior half of the supratemporal arch and medially, it forms, together with the parietal, the posteromedial margin of the supratemporal fenestra. The occipital portion of the squamosal is flange-like and meets the supraoccipital medially and the exoccipital-opisthotic complex ventrally. Laterally, the descending process of the squamosal extends downwards to the quadrate condyle.

The presence of the quadratojugal is uncertain.

The quadrate is of limited exposure. Its posterior surface is concave. The lateral portion of the condyle appears slightly larger than the medial portion.

The occiput is closed and plate-like, typical to eosauroptrygians (Rieppel, 2000). No distinct occipital crest present. The surface of the supraoccipital is flat, without a medial ridge. No sutures between the braincase bones are clearly recognized owing to poor preservation on the new specimen. Both the holotype and new specimen show the occipital condyle locating at the same level as the mandibular condyles of the quadrate.

The paired vomers are elongated and bar-like. They form the medial margins of the internal choanae anterolaterally and contact the palatines posterolaterally. They extend posteriorly and suture with the pterygoids at a level nearly below the anterior margins of the orbits.

The palatine is a broad plate and extends substantially parallel to the direction of the dentary. Its anterior part forms the posterior margin of the internal choana. Though there are some cracks, its suture with the pterygoid is clear, being lineal and oblique in direction.

The ectopterygoid lies posterior to the palatine and point to the infratemporal fenestra. It meets the anterolateral side of the transverse process of the pterygoid medially. The ectopterygoid is also present in *Diandongosaurus* (Sato et al., 2014), but not in other Chinese pachypleurosaur-like forms such as *Dianopachysaurus* (Liu et al., 2011), *Dawazisaurus* (Cheng et al., 2016) and *Keichousaurus* (Holmes et al., 2008).

The pterygoids form most of the palate. Anteriorly, more than three-quarters of the pterygoids are widely spaced along the midline, but the posterior quarter meets on the midline with unclear suture (Shang and Li, 2015: fig. 2). The anteriorly narrow end of the pterygoid meets the vomer. The quadrate ramus extends posterolaterally, and broadly contacts the pterygoid ramus of the quadrate at the position lateral to the occipital region.

Two hyobranchia are preserved on the ventral surface of the pterygoids. They are thin, stick-

like, with an anterior portion slightly thicker than the posterior portion as in those of some other eosauropterygians, such as the European pachypleurosaurs (Carroll and Gaskill, 1985; Sander, 1989), *Keichousaurus* (Holmes et al., 2008), and some nothosaurs (Li and Rieppel, 2004).

Mandible The mandibular symphysis is short, comparable with that of *Keichousaurus* (Lin and Rieppel, 1998; Holmes et al., 2008), and much shorter than *Diandongosaurus* (Sato et al., 2014).

The dentary extends posteriorly to a level exceeding the half way of the mandibular ramus. Posteroventrally, it overlaps the angular and tapers into a pointed end. Posterolaterally and posterodorsally, it meets the angular and surangular with interdigital sutures.

Only the anterior portion of the splenial is exposed in the holotype. It takes part in the forming of the mandibular symphysis as in *Diandongosaurus* (Sato et al., 2014).

The surangular forms the dorsal half of the posterior portion of the mandible and the dorsolateral edge of the retroarticular process. The angular is longer than the surangular and forms the posteroventral half of the mandible and the ventrolateral edge of the retroarticular process. Anteromedial to the angular, a triangular prominent projecting dorsally indicates the presence of the coronoid process.

The anterior portion of the articular is broad and forms most of the articular fossa. The latter is divided into two parts, matching the divisions of the quadrate condyle. The retroarticular process is well-developed, slightly longer than the length of the supratemporal fenestra. The dorsomedial surface of the retroarticular process is concave and its posterior end is truncated.

Dentition There are five premaxillary teeth, of which the anterior four are enlarged and fang-like, but not as large as the king-sized premaxillary teeth of the *Diandongosaurus* (Shang et al., 2011) and the fifth is possibly smaller as *Nothosaurus* (Rieppel, 2000).

The third maxillary tooth is fang-like which is as large as the premaxillary teeth. The maxillary teeth anterior and posterior to this fang-like tooth are much smaller and of similar size. The maxillary tooth row extends posteriorly almost to the level of the posterior end of the orbit. It is difficult to know the exact number of the maxillary teeth due to the occlusion of the jaws. Based on the preserved teeth and their spaces in both the holotype and the new specimen the maxilla possibly bears 15 teeth.

It is evident that four fang-like teeth are present within the symphyseal region of the mandible. It is uncertain if the fifth dentary tooth is also fang-like. It is impossible to establish an exact tooth count behind the symphyseal fangs owing to the tight occlusion of the lower jaw with the upper jaw.

All the exposed teeth are sub-conical and curve medially and slightly posteriorly, with fine striations on the crown surface.

Axial skeleton The last cervical or the first dorsal vertebra cannot be determined due to the poor preservation of ribs in the shoulder girdle region in the new specimen, although the count of 45 pre-caudal vertebrae is the same as in the holotype (Shang and Li, 2015). The presence of four vertebrae was inferred in the sacral region of the holotype, but the number of

four sacral vertebrae can be confirmed in the new specimen. In this case, it is most likely that the new specimen also had 23 cervical, 18 dorsal, and four sacral vertebrae as in the holotype. For the tail, 36 caudal vertebrae are preserved in the holotype (Shang and Li, 2015), while 41 caudals are preserved in the new specimen (Fig. 1). The zygapophyseal pachyostosis is not evident in the exposed sections of the vertebral column and all ribs clearly lack such a swelling in both the holotype and the new specimen.

The atlas is represented by a small stumpy atlantal centrum and two relatively large irregular arched atlantal neural arches in the holotype. The small axial odontoid process is also well exposed in the holotype. It is multi-prism-shaped and shorter than the atlantal centrum. A very similar bone was illustrated for *Neusticosaurus pussilus* (Sander, 1989: fig.14).

As the following cervical vertebrae, the axial centrum is cylinder-shaped and its ventral surface is concave. It is slightly shorter than that of cervical 3 in the holotype. The preserved post-zygapophyses of the axis are flat and broad.

In the holotype, the anterior cervical centra are slightly increases in length/width ratio, which is about 2.5 in the anterior cervical vertebrae (from the third to 11th), but the ratio decreases dramatically from the 12th, and it diminishes to 1.7 for the 20th cervical. The ventral surface of the centrum is smooth, without longitudinal keel and subcentral foramina. The new specimen shows that the cervical neural arch possibly bears a wide neural spine.

Axial rib is not preserved in both the holotype and the new specimen.

From the 3rd to 11th cervical vertebrae, the associated ribs are nearly constant in size and similar in shape. They developed a distinct anterior process close to the articular heads, which is longer than the shaft. From the 12th cervical, rib gradually increases in length but its anterior process gradually decreases in length. The anterior process entirely disappears from the 18th rib. The rib distal ends are tapered till the 23th.

The size and shape of the dorsal vertebrae are not distinctly different from the cervicals in the pectoral region.

Most of the dorsal vertebrae are covered by the elements of the gastralia, and the exposed ones show a distinctly constricted centrum. The posterior dorsal vertebrae are slightly longer than the anterior ones in the holotype.

The shape of the dorsal neural arches of the new specimen is obscured because of the poor preservation, but it is clear that the postzygapophyses are broad and flat, the transverse processes are short, and the zygospheny-zygantrum articulation is present.

All 18 pairs of the dorsal ribs are exposed in both the holotype and the new specimen (Fig. 3). The first dorsal rib of the holotype clearly shows a truncated distal end, with a shoulder section slightly wider than its distal end. In the middle part of the trunk, the ribs are of nearly constant size, whereas the last three (from the 16th to 18th) dorsal ribs decrease in size again as they approach the sacrum.

Four sacral vertebrae identified in the new specimen. There is no significant difference between the sacral and dorsal vertebrae in outline. Among the four sacral ribs of the new

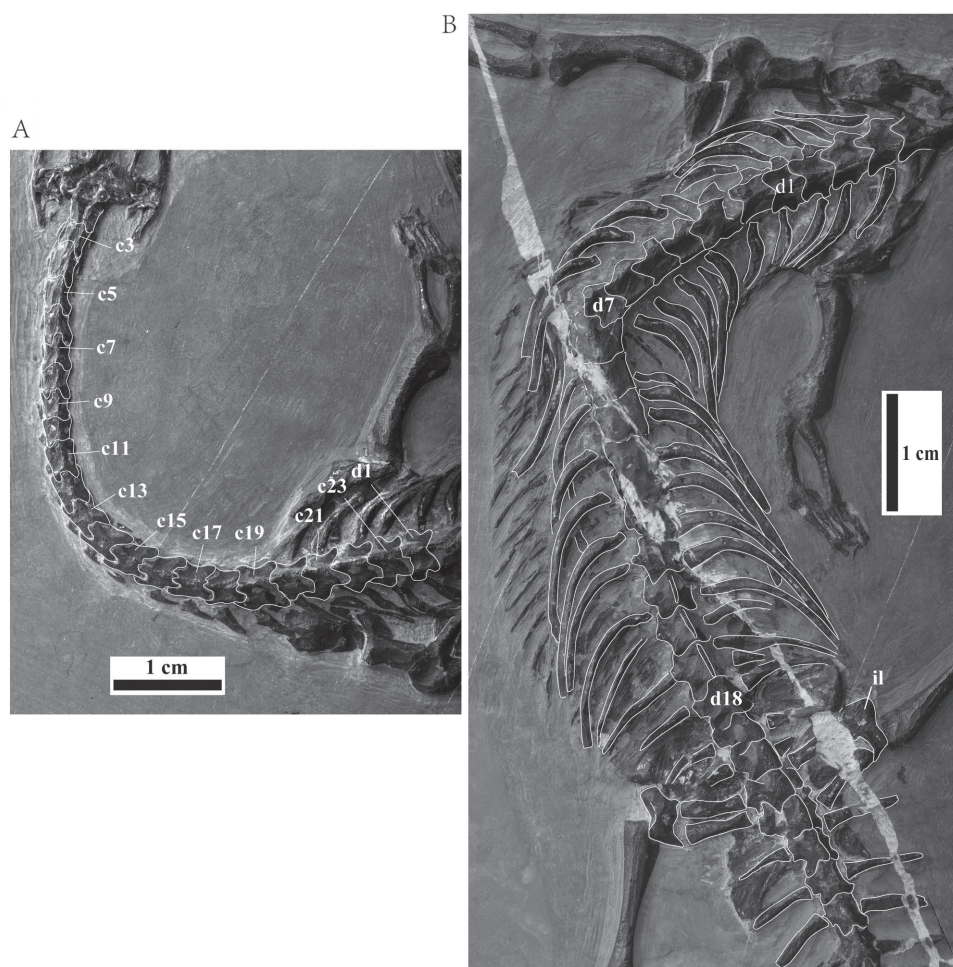


Fig. 3 Cervical (A) and dorsal (B) vertebrae of *Dianmeisaurus gracilis* (IVPP V 17054) in dorsal view

Abbreviations: c3–23. the 3rd–23th cervical vertebra 第3–23节颈椎;

d1, 7, 18. the 1st, 7th, 18th dorsal vertebra 第1、7、18节背椎椎体; il. ilium 髌骨

specimen, the first and second are incomplete, whereas the third is as long as the fourth (5 mm in length). The sacral ribs are bar-shaped and slightly expanded at their distal end.

A total of 36 caudal vertebrae are preserved in articulation in the holotype and 41 in the new specimen. The last of the preserved caudal vertebra is less than 2 mm in length in the holotype, which suggests that the missing tip of the tail may have only contained the last few caudals in the holotype. The last caudal vertebra of the complete tail of the new specimen is less than 1 mm.

The caudal vertebrae gradually decrease in size caudally. The caudal centra are cylindrical and constricted medially. The neural spines are low and strongly oblique posteriorly.

The first five caudal vertebrae bear long and slender, laterally directed transverse processes, which are gradually shortened in length posteriorly and are followed by four caudals with very short and triangle-shaped transverse processes.

Each gastral set consists of five elements as in other eosauropterygians. The angle degree of

the V-shape median elements increases caudally. The lateral elements bear a pointed distal end, which differs from the broadened end of the elements in *Diandongosaurus* (Sato et al., 2014).

Appendicular skeleton The pectoral girdle is fully exposed in the holotype (Fig. 4A). The narrow medial portion of the clavicle meets its counterpart to exclude the interclavicle from the anterior edge of the pectoral girdle; the wide lateral portion of the clavicle developed a sharply triangle-shaped anterior process at its anterolateral corner. This anterior process is placed at the same position as that in *Diandongosaurus* but it is much stouter and blunter distally. Such an anterior process was considered as a diagnostic character for *Dianmeisaurus gracilis* by Shang and Li (2015) and unequivocally present in the new specimen (Fig. 4B). The posterolateral process of the clavicle overlaps the anteromedial dorsal aspect of the scapula, showing a typical pattern of sauropterygians.

The interclavicle is rhomboidal and lacks a posterior process.

The scapula has a constriction separating a ventral glenoidal portion from a posteriorly directed dorsal wing. The scapula dorsal process is rod liked and tapers to a blunt tip, with a rod length as long as the glenoidal portion.

The coracoid shows a rounded proximal head and a strongly concave anterior margin opposing the less distinctly concave posterior margin. The coracoids of both sides meet ventrally in a well-defined suture.

Of the pelvic girdle, the ilium is not preserved in the holotype, but it is well exposed in dorsal view in the new specimen (Fig. 3B). It develops a short and tapering posterior process and the broadened ventral portion to contribute the formation of the acetabulum.

The two ischia and two pubes are preserved in articulation in the holotype (Shang and Li, 2015: fig. 3B). Their morphology conforms to the general pattern of nothosaurs (Romer, 1956; Rieppel, 2000).

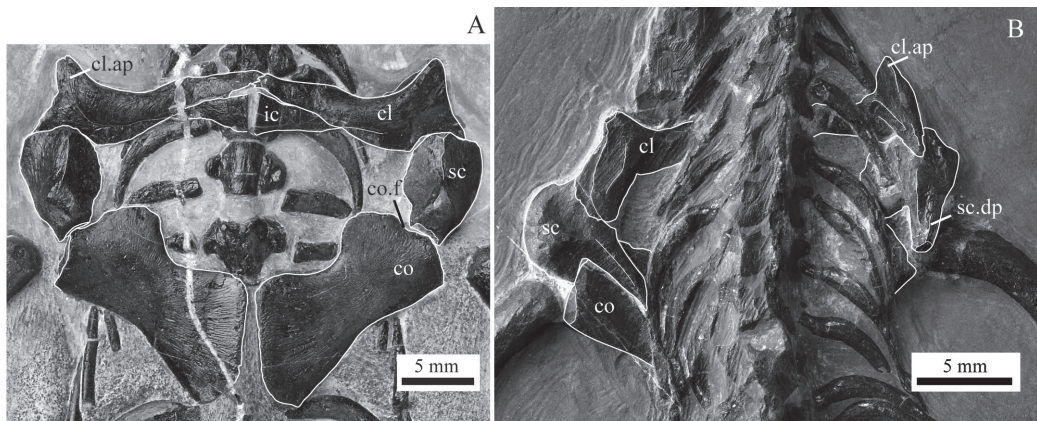


Fig. 4 Pectoral girdle of *Dianmeisaurus gracilis* in ventral (A, IVPP V 18630, holotype) and dorsal (B, V 17054) views

Abbreviations: cl. clavicle 锁骨; cl.ap. anterior process of clavicle 锁骨前突; co. coracoid 乌喙骨; co.f. coracoid foramen 乌喙孔; ic. interclavicle 间锁骨; sc. scapula 肩胛骨; sc.dp. dorsal process of scapula 肩胛骨背突

The pubis shows weakly concave anterior and posterior margins. The obturator foramen is not closed, with an open slit at their sutures with the ischia near the acetabular margin of the bones (see Shang and Li, 2015: fig. 3B).

The ischium shows a narrow acetabular portion, a weakly concave anterior margin, a strongly concave posterior margin, and a widely expanded medial portion with a convex medial margin (see

Shang and Li, 2015: fig. 3B).

There are no notable differences in the limb morphology between the holotype and the new specimen (Figs. 5, 6). The limbs are long and slender, with the forelimb slightly shorter than the hindlimb.

The humerus is shorter than the femur but relatively stouter than the latter. It shows a concave medial (preaxial) margin, a broadly expanded distal portion, and a weakly sigmoidal appearance. The entepicondylar foramen is well set off from the distal articular facet and a distinct ectepicondylar groove is present.

The ulna is as long as the radius, but stouter than the latter. The proximal head of the ulna is more expanded than the distal end. The proximal end of the radius is slightly wider than the distal end.

In the holotype, the carpus comprises three ossified rounded elements, i.e., the intermedium, the ulnare, and the fourth distal carpal, in the right forelimb, but only two ossified carpal elements, i.e., the intermedium and the ulnare, are preserved in the left forelimb, with the fourth distal carpal missing in this forelimb. The fourth distal carpal is not observed on both left and right forelimbs in the new specimen.

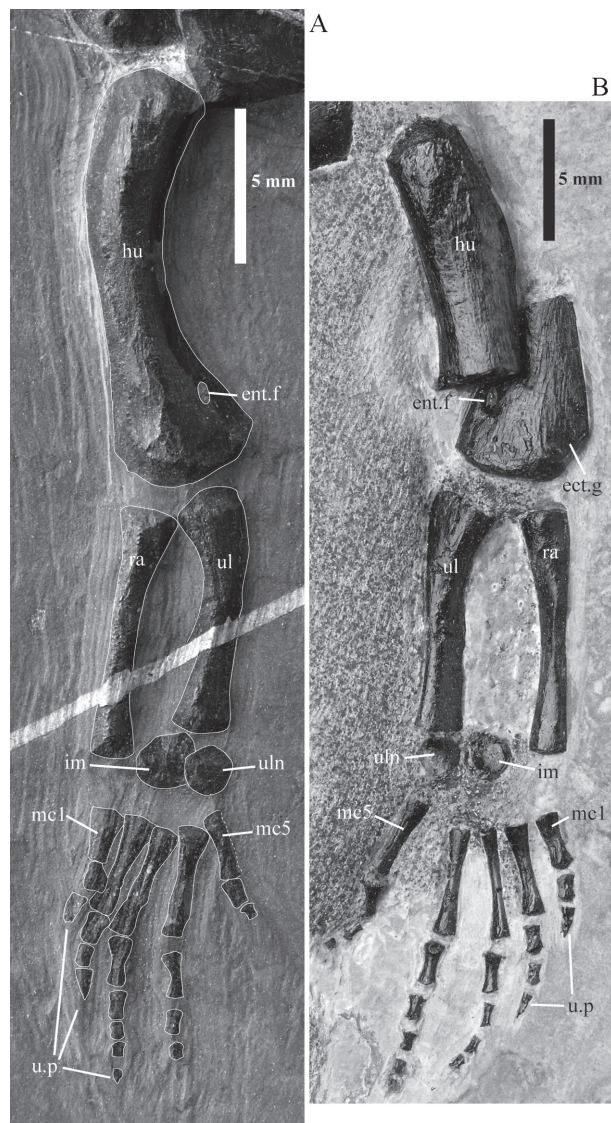


Fig. 5 Left forelimb of *Dianmeisaurus gracilis* in dorsal (A, IVPP V 17054) and ventral (B, V 18630, holotype) views

Abbreviations: ect.g. ectepicondylar groove 外髁沟; ent.f. entepicondylar foramen 内髁孔; hu. humerus 肱骨; im. intermedium 中间腕骨; mc1, 5. metacarpal 1, 5 第一、五掌骨; ra. radius 桡骨; ul. ulna 尺骨; uln. ulnare 尺腕骨; u.p. ungual phalange 爪指骨

The 1st metacarpal is much shorter and slightly broader than the others. The 3rd metacarpal is as long as the 4th metacarpal in the holotype, but is the longest in the new specimen, which suggests an asymmetrical development of the two metacarpals given the fact of the size difference between the two specimens.

The phalangeal elements are completely preserved in digitals 1 to 3 and 5, but missing the ungual in the fourth digit in the right manus of the holotype. The complete fourth digit of the left manus in the new specimen bears five phalangeal elements. In this case, the phalangeal formula of the forelimb counts for 2-3-5-5-3 in *D. gracilis*. All preserved ungual phalanges in the forelimbs show no distinct expansion that is seen in *Diandongosaurus* (Shang et al., 2011).

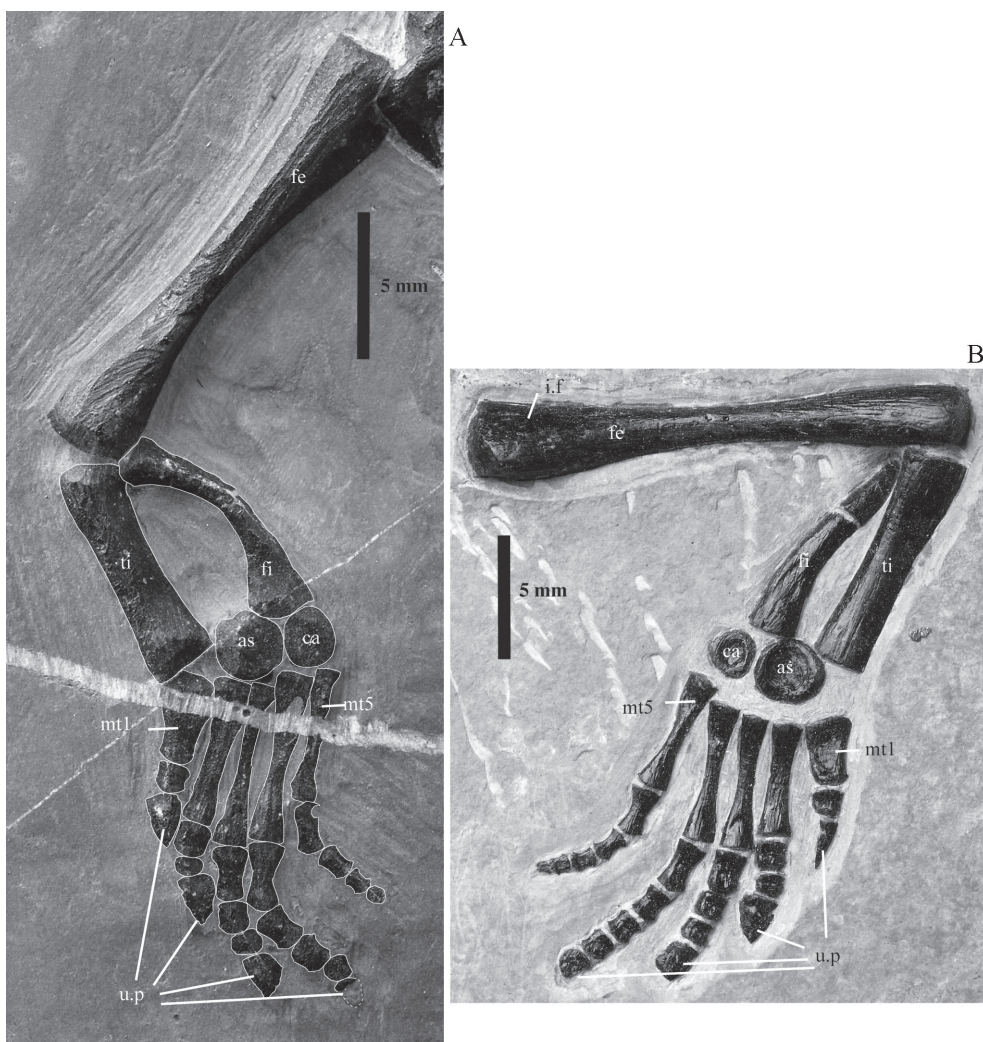


Fig. 6 Left hindlimb of *Dianmeisaurus gracilis*

in dorsal (A, IVPP V 17054) and ventral (B, V 18630, holotype) views

Abbreviations: as. astragalus 距骨; ca. calcaneum 跟骨; fe. femur 股骨; fi. fibula 腓骨;

i.f. intertrochanteric fossa 转子窝; mt 1, 5. metatarsal 1, 5 第一、五趾骨; ti. tibia 胫骨;

u.p. ungual phalange 爪趾骨

The femur is slender and sigmoidal in outline (Fig. 6). The femoral shaft is straight and biconcave. The proximal head is expanded and slightly wider than the distal head. A very shallow intertrochanteric fossa appears present.

Of the two lower limb elements, the fibula and tibia are approximately of same length, and the tibia is wider than the fibula. The fibula is slender and strongly curved, which contracts with the rather straight tibia.

In both the holotype and new specimen, two tarsal elements are ossified, i.e., the rounded astragalus and calcaneum. The latter is smaller than the former and lies between the distal end of the fibula and metatarsal 5.

The 1st metatarsal is distinctly shorter and broader than all the others. Its proximal head is markedly expanded. The 4th metatarsal is the longest in the metatarsal series. The phalangeal elements are cylindrical, slightly constricted at the mid shaft, and get shorter in length towards the tip of the digits. The ungual elements are well-developed in the 1st to 4th digits of the new specimen. They are markedly expanded as in *Diandongosaurus* (Shang et al., 2011), with a size distinctly larger than their preceding phalanges.

The phalangeal elements of the hindlimbs are completely preserved in the holotype, except for digit 4 where the ungual is missing. With the addition of the ungual to digit 4, the phalangeal formula of the hindlimb should have counted for 2-3-4-5-5 in *D. gracilis*.

3 Discussion

3.1 Evidences supporting the assignment of the new specimen to *Dianmeisaurus gracilis*

Although the holotype and new specimen are preserved in different views, the skulls of both specimens display a similar appearance. They are comparable in having moderately developed fang-like teeth in the premaxillary, maxilla, and the dentary, and a very anteriorly positioned naris. The distinctly narrow interorbital septum of the holotype is clearly true in the new specimen. In the holotype, we estimated that the narrow interorbital septum was half the width of the intersupratemporal region in terms of its ventral exposure. The new specimen shows an even narrower interorbital septum, less than 1/3 of the width of the intersupratemporal region. This is unique among known Chinese pachypleurosaur-like forms. In addition, in both the holotype and the new specimen the broad intersupratemporal region is morphologically comparable to that of *Keichousaurus* but differs from the latter in that there is no constriction at the posterior end of the region.

The new specimen is also identical to the holotype in the postcranial region. It has 41 presacral vertebrae, in contrast to 39 in *Dianopachysaurus*, 38 in *Diandongosaurus*, and 36 in *Dawazisaurus*; its ribs are not pachyostotic; the first five caudal ribs are elongate and blunt distally; and the clavicle possesses a stout anterolateral process, differing from that of *Diandongosaurus* in which the process is slender and shaper. In addition, the new specimen also shares the following limb characteristics with the holotype: the long and slender profile,

the presence of the entepicondylar foramen, the proximal head of the ulna expanded and wider than the distal end, the presence of two ossified tarsals and the rounded astragalus, the broadened 1st metatarsal. The only distinct difference is the number of the ossified carpals: three in the holotype and two in the new specimen. This may have reflected an ontogenetic variation, i.e., the fourth distal carpals had not started to co-ossify yet in the smaller new specimen which is 65 mm shorter than the holotype in total length. Therefore, it is most probable that the number difference of the carpals between the holotype and the new specimen does not represent a true fact.

3.2 Phylogenetic position of *Dianmeisaurus*

The data matrix used here is derived from that of Shang and Li (2015). In our analysis, *Dawazisaurus* (Cheng et al., 2016) was also included and the character scores of *Dianmeisaurus* were modified based on new specimen (Appendix 1). With the addition of *Dawazisaurus*, the data matrix has 42 taxa and 139 characters.

The data matrix was analyzed using PAUP* (version 4.0b10; Swofford, 2002). Multistate characters were treated as unordered and all characters were equally weighted. A heuristic search of all 42 taxa yielded 207 most parsimonious trees (MPTs) with 750 steps, a CI of 0.4840, and a RI of 0.6318. Different from the results of Sato et al. (2014) and Shang and Li (2015), the strict consensus of the 207 MPTs indicated that the branching patterns changed drastically and the relationships among the Chinese pachypleurosaur-like taxa, the European pachypleurosaurs and the members of Nothosauroidae were all unsolved.

To test if the fragmentary taxa (*Kwangsisaurus*, *Chinchenia* and *Sanchiaosaurus*) would have influenced the results or not, we did a second analysis with the three fragmentary taxa excluded. A heuristic search of the removal of the three taxa yielded 8 shortest trees, with 706 steps, a CI of 0.5142, and a RI of 0.6676. The result of this analysis is largely comparable to that of the second analysis of Shang and Li (2015), supporting the sister-taxon relationship between *Dianmeisaurus* and *Diandongosaurus* (Fig. 7). The Chinese pachypleurosaur-like *Dianmeisaurus*, *Diandongosaurus*, *Majiashanosaurus*, *Dianopachysaurus*, *Keichousaurus*, and *Dawazisaurus* formed a monophyletic clade and more closely related to the Nothosauroidae than to the European pachypleurosaurs. *Qianxisaurus*, *Wumengosaurus*, and *Hanosaurus* formed a set of successive sister-groups towards a clade containing the European pachypleurosaurs, the Nothosauroidae and the aforementioned six Chinese pachypleurosaur-like forms. The differences between Shang and Li (2015) and the current study are that *Keichousaurus* is more basal in position than *Dianopachysaurus* within the Chinese clade and *Hanosaurus* is more remotely related to the Nothosauria than any of other Chinese pachypleurosaur-like forms.

The sister-group relationship between *Dianmeisaurus* and *Diandongosaurus* is supported by three unequivocal characters under ACCTRAN optimization, i.e., the absence of pachyostosis in the dorsal ribs [72(0)], the presence of an anterolateral process in the clavicles [80(2)], and three carpal ossifications [137(1)].

The three fragmentary taxa from China (*Chinchenia*, *Kwangsisaurus*, and

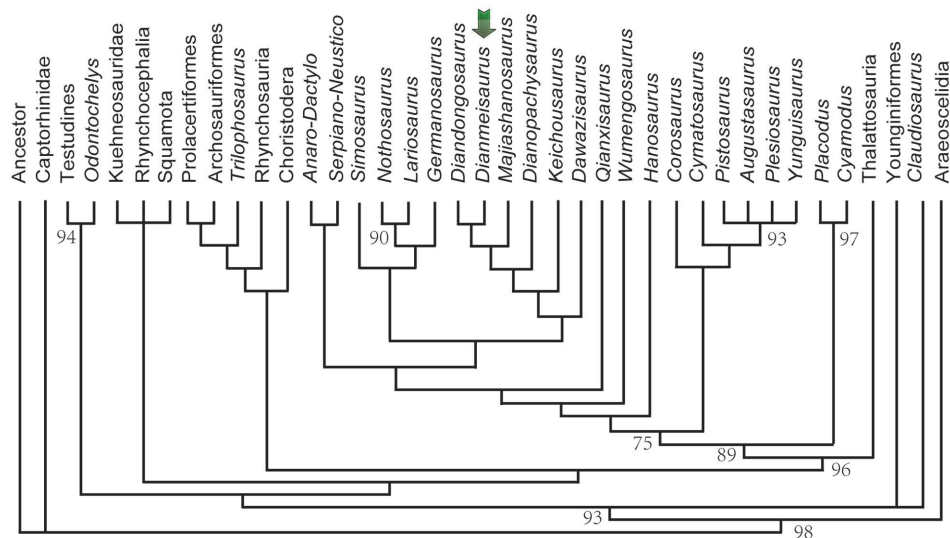


Fig. 7 Cladogram depicting the phylogenetic relationships of *Dianmeisaurus*

Strict consensus tree of 8 MPTs of the analysis without *Kwangsisaurus*, *Sanchiaosaurus* and *Chinchenia*

Arabic numbers indicate the bootstrap support values above 75%. Abbreviations: *Anaro.* *Anarosaurus*;

Dactylo. *Dactylosaurus*; *Neustico.* *Neusticosaurus*; *Serpiano.* *Serpianosaurus*

Sanchiaosaurus) have different phylogenetic positions and are never grouped together in previous studies (Rieppel, 1999; Holmes et al., 2008; Sato et al., 2014; Shang and Li, 2015; Cheng et al., 2016). As tested in the two analysis of this study, here is the case again that the poorly preserved taxa are largely influenced the internal branching patterns of the European pachypleurosaurs, Nothosauroidae, and Chinese pachypleurosaur-like forms.

3.3 Morphological comparisons of the small sized eosauropterygians from the Luoping Fauna

Up to now, four small-sized eosauropterygian taxa have been described from early Middle Triassic of Luoping. They are *Diandongosaurus*, *Dianopachysaurus*, *Dianmeisaurus*, and *Dawazisaurus*. All of them have an adult body length shorter than 50 cm and share the characters below: a slender body with little specialized limbs, a skull with a large orbit and a small supratemporal fenestra, as well as a relatively elongate neck and tail.

Among these small eosauropterygians, the holotype of *Dianopachysaurus dingi* should be a juvenile, as indicated by the unfinished ends of the limb bones and the weak ossification of the skull bones. As preserved, the snout-pelvis (pre-caudal) length is about 100 mm and the skull is 23 mm long in the holotype of *D. dingi* (Liu et al., 2011). The corresponding lengths reach separately to 194, 24 mm in the holotype of *Diandongosaurus acutidentatus* (IVPP V 17761), 176 and 22 mm in the holotype of *Dianmeisaurus gracilis* (V 18630), and 236 and 36 mm in the holotype of *Dawazisaurus brevis* (Cheng et al., 2016). Although *D. dingi* is based on a juvenile skeleton, its holotype is distinct in several diagnostic features, such as the broad parietal with a weak constriction at the posterior end, the presence of at least four

carpal ossifications (Liu et al., 2011). The holotype and the new specimen of *D. gracilis* are larger than the holotype of *D. dingi* but the carpals of the latter have fewer ossified elements, indicating that they could not be adults of *Dianopachysaurus*. In addition, as shown in the new specimen, the broad intersupratemporal region does not have a constriction at the posterior end in *D. gracilis*. The relatively long snout, the lack of the anterolateral process of the clavicle and the pachyostotic ribs further distinguish *Dianopachysaurus* from *Dianmeisaurus*.

D. brevis (Cheng et al., 2016) has a short trunk (16 dorsal vertebrae), very small pre- and postzygapophyses and five ossified distal carpals. It is also distinct from *D. gracilis*.

Although *Dianmeisaurus* is phylogenetically close to *Diandongosaurus*, the latter has the following autapomorphies which are demonstrably absent in the former: the nasals reduced and separated from one another by the premaxillae, the large nasal processes of the premaxillae extending backwards to insert into the frontal, the frontal excluded by the prefrontal-postfrontal contact from the dorsal margin of the orbit, the parietal skull table weakly constricted, the mandibular articulation displaced to a level distinctly behind the occipital condyle, the premaxilla excluded from the margin of the internal choana, and the intertrochanteric fossa distinct but reduced. The *Dianmeisaurus* differs from *Diandongosaurus* in the following autapomorphies: the frontals are paired, the coronoid process of lower jaw is distinct, the cervical centra are rounded, there are four sacral ribs, the clavicles and interclavicle are in a simple overlapping contact, and the external naris is retracted, with a longitudinal diameter distinctly less than half the longitudinal diameter of the orbit. In addition, the premaxillary fangs are not king-sized, the supratemporal fenestra is elongated elliptic, the interorbital septum extremely narrow, and the anterolateral process of the clavicle is much stouter.

4 Systematic paleontology

Sauropterygia Owen, 1860

Eosauropterygia Rieppel, 1994a [sensu Rieppel, 2000]

Dianmeisaurus Shang & Li, 2015

Dianmeisaurus gracilis Shang & Li, 2015

(Figs. 1–6)

Holotype IVPP (Institute of Vertebrate Paleontology and Paleoanthropology) V 18630, a nearly complete skeleton with the skull articulated and preserved in ventral view.

Referred specimen IVPP V 17054, a nearly complete skeleton with the skull articulated and preserved in dorsal view.

Locality and horizon Da'aozi Village, Luoping County, Yunnan Province, China. The Upper Member of the Guanling Formation in the conodont *Nicoraella kockeli* Zone; Pelsonian, middle Anisian, Middle Triassic (Zhang et al., 2009).

Emended diagnosis A small eosauropterygian with a total length less than 50 cm and differs from others in the combination of following characters: snout (preorbital region) shorter

than postorbital region and orbit in length; rostrum with no constriction; external naris closer to the anterior end of the rostrum than to the orbit; supratemporal fenestra elliptic and much smaller than orbit; interorbital septum extremely narrow; intersupratemporal septum about three times the interorbital septum; pineal foramen anteriorly positioned; posterior margin of the skull roof deeply V-shaped; premaxillary and anterior dentary teeth fang-like but not king-sized; maxilla with one fang-like tooth behind one or two distinctly smaller conical teeth; vertebral column consisting of 23 cervical, 18 dorsal, four sacral, and 41 caudal vertebrae; anterior caudal ribs 1 to 5 elongate and with blunt distal end; clavicle with a stout anterolateral process; entepicondylar foramen present; three ossified carpals; two ossified tarsals; first metatarsal broaden; pes unguis phalanx extremely expanded; manual phalangeal format 2-3-5-5-3; and pes phalangeal format 2-3-4-5-5.

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纤细滇美龙(*Dianmeisaurus gracilis* Shang & Li, 2015)新材料

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摘要: 根据一件产自云南罗平中三叠世关岭组II段的新标本并结合产自相同地点和地层中的模式标本对纤细滇美龙(*Dianmeisaurus gracilis* Shang & Li, 2015)进行了详细研究。原模式标本暴露其腹面, 而新标本暴露其背面, 两者互相补充提供了更完整、精确的纤细滇美龙解剖学信息。新材料揭示该种具有非常短小的吻部, 眶前区的长度不仅短于眶后区长度, 甚至短于眼眶的长度; 外鼻孔小且位置靠前, 即鼻孔前区的长度短于鼻孔后缘与眼眶前缘之间的距离; 由两额骨构成的眼眶间隔非常狭窄, 宽度小于顶骨平台宽度的1/3; 额骨前后两端均具渐尖的突起; 顶骨后部不收缩, 顶骨平台后缘呈深V型。补充了新信息和包含更多属种(如*Dawazisaurus*)后的系统发育学分析支持了之前滇美龙和滇东龙互为姊妹群的结论, 同时它们和马家山龙、滇肿龙、贵州龙和大洼子龙一起构成了一个仅由中国的属种组成的单系类群。与欧洲肿肋龙类群(*Dactylosaurus*, *Anarosaurus*, *Serpianosaurus*和*Neusticosaurus*)相比, 这一单系类群与幻龙类有更近的亲缘关系。

关键词: 云南罗平, 中三叠世, 安尼期, 始鳍龙类, 纤细滇美龙

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Appendix 1 Data matrix for *Dianmeisaurus*

The principle phylogenetic analysis described in the text used the data matrix of Sato et al. (2014) with the addition of *Majiashanosaurus* (Jiang et al., 2014) and *Dawazisaurus* (Cheng et al., 2016). Listed below are the 139 character codings for *Dianmeisaurus*

1000000020	0230111301	11000120??	2?0?1011??	??0?00?110	000010011?	1101?00?0?
1021011012	1021010211	0111110220	11?1121110	0011200000	0000?00000	00200?10?